

INVESTIGATION OF SOME FUNCTIONAL ANATOMICAL AND DEVELOPMENTAL ASPECTS OF PTEROSAURS

Theses of the PhD dissertation

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GENERAL INTRODUCTION

The enigmatic clade of pterosaurs, the first group of vertebrates which was capable of powered flight, is a dominant element of the Mesozoic terrestrial faunas. Despite that Pterosauria has been a well-known group since the beginning of the 19th century, due to their highly specialized anatomical and morphological flight adaptations several questions concerning their paleobiology remained still open. Since flight-related limb modifications are unlike those of the two extant vertebrate flyers, birds and bats, the aerodynamics and biomechanics of the pterosaurian flight is one of the most intensely investigated fields in pterosaur research. Aspects of feeding-mechanics are of crucial importance in lifestyle-reconstructions and were, accordingly, in the spotlight of scientists on diverse occasions. With the advent of new techniques in fossil bone histology the interest in pterosaurian ontogeny and life-history strategies has also been renewed. The main objectives of my dissertation were to elucidate some details of these three independent issues, namely I. the potential for cranial kinesis in the pterosaurian skull; II. the mechanism of the wingfinger extension; III. the debated ontogeny and life history of a well-known pterosaurian genus. Considering the independent nature of these subjects, here I follow the structure of the dissertation and discuss the main points of the thesis separately in three different sections.

I. Potential for intracranial movements in the pterosaurian skulls

Cranial kinesis which refers to intracranial movements between skull elements excluded that of the lower jaw occurs in many vertebrate groups from fish to birds (Frazzetta, 1962; Iordansky, 1990). The most widespread form and probably the prerequisite of all other types of kinesis is streptostyly. Streptostyly describes the anteroposterior rotation of the quadrate (the skull element that connects the lower jaw to the cranium) about the otic joint (Metzger, 2002). Among the known forms of cranial kinesis only this type has been proposed to have occurred in two pterosaur species, the Late Triassic *Eudimorphodon ranzjii* (Wild, 1978) and the Early Jurassic *Dorygnathus banthensis* (Arthaber, 1919). Based on the firmly ossified skulls characterizing more derived, pterodactyloid pterosaurs, most pterosaurologists have regarded the pterosaurian skull as universally akinetic (e.g. Wellnhofer, 1978).

In spite of this it is worth reconsidering the potential for cranial kinesis in pterosaurs for two reasons. First, according to most recent cladistical analyses (e.g. Hone & Benton, 2008) pterosaurs are the sister group of dinosaurs, for which cranial kinesis has been proposed on

several occasions (e.g. Norman & Weishampel, 1985). Thus, the plesiomorphic nature of streptostyly and its presumed presence in dinosaurs might imply that it could have appeared in pterosaurs as well. Second, certain morphological attributes of some pterosaurian skulls suggest that some cranial elements could have been capable of significant movement relatively to each other.

Materials and methods

First I evaluated the plausibility of cranial kinesis based on phylogenetic considerations. To analyse the probability in a phylogenetic context I applied EPB method (Extant Phylogenetic Bracket) described by Witmer (1995). Thereafter, following the comparative anatomical and morphological method of Holliday & Witmer (2008), I examined the skulls of 27 different genera. The investigation was based on the demonstration of the presence or absence of morphological correlates of cranial kinesis. Finally I evaluated the data in a phylogenetic context.

Results and conclusions

- The use of EPB in predicting the kinetic potential of pterosaurian skulls is inconclusive because 1) the phylogenetic position of the clade is too ambiguous; 2) the distance between pterosaurs and their presumed closest extant relatives is very large; 3) pterosaurs as well as their bracketing taxa represent very high taxonomic levels, thus the variability in the examined trait can be very high even within the extant bracketing taxa themselves.
- Whereas skeletally mature derived pterodactyloids have completely fused, rigid and doubtlessly akinetic skulls, skeletally immature derived pterodactyloids and more basal pterosaurs possess key features in the morphology of their otic and basal joints that are suggestive of streptostyly.
- There seems to be an evolutionarily-informative trend in the degree of cranial ossification where it is low in most non-pterodactyloids (here named bifenestratans), intermediate in *Rhamphorhynchus* and Archaeopterodactyloidea, and high in derived pterodactyloids.
- However, another crucial anatomical requirement of a kinetic skull, the permissive kinematic linkage is absent in all pterosaurian taxa.
- The fact, that the presence of permissive kinematic linkages in the skull is also a prerequisite of all types of cranial kinesis, provides hard evidence that all members of Pterosauria had akinetic skulls.
- The presence of the morphological attributes indicative of intracranial movements in some pterosaurs could either be of mechanical and/or ontogenetic importance, or it might be

considered as the morphological remnant of a real, kinetic skull possessed by the still unknown ancestor of pterosaurs.

II. New models for the mechanism of wing extension in pterosaurs

Operating the wings with muscles requires constant energy input and neural control in all powered flying animals. The significant increase in the amount of muscles that enables this energy consuming locomotory type however means increase in body mass as well, which in turn makes flight more difficult or might even prohibit it. The convergent evolution resulted in similar solutions to these issues in the two extant groups of flying vertebrates, birds and bats – the biomechanical automatism built in their skeletal, muscular and connective tissue systems (Hill & Smith 1984; Brown *et al.* 1995). Owing to the biomechanical automatism a significant portion of the phases of wing operation becomes passive; hence the energy requirements of flight as well as the need for extra muscle mass decrease (Vazquez, 1994; Brown *et al.* 1995). Thus, the largely automated and passive wing operation seems to be a necessary element of powered flight in all volant vertebrates, including pterosaurs, among which we find the largest flying animals ever lived on Earth.

Among the actively flying vertebrates pterosaurs possess the longest rigid lever arm in the leading edge of their distal wing. This lever arm, the so called wingfinger (extremely elongated fourth finger of the manus) solely supported distally the extensive wing membrane, thus the extended wing finger must have experienced significant loads in form of 1) profile drag; 2) tension in the elastic wing membrane; 2) tension in the trailing edge structure which all acted to flex the wingfinger. Hence wingfinger extension must have been considerably greater energy expenditure in pterosaurs than it is in birds or bats. Wing extension in pterosaurs could be described by models that perform the anatomically possible and energetically most efficient mechanism of wingfinger extension during steady flight.

Results and conclusions

- The mechanism of wingfinger extension in pterosaurs can be demonstrated by a main model and an accessory model on a hypothetical pterosaur. In the main model the presence of a propatagial ligament or ligamentous system is hypothesized which, as a result of the elbow extension, automatically performs and maintains the extension of the wing finger during flight and prohibits the hyperextension of the elbow. The second model has a co-operating bird-like propatagial ligamentous system and bat-like tendinous extensor muscle system on the forearm of the hypothetical pterosaur.

- Both models provide solution for the problems related to powered flight, since both: 1) decrease the essential amount of distal wing muscles thereby decreasing the total body mass, as well; 2) prevent the dangerous hyperextension of the elbow; 3) automate wing finger extension thereby reducing the metabolic costs (active muscle work and neural control) of pterosaurian powered flight; 4) ensure the orderly and secure accomplishment of the movement series of wingfinger extension.
- Although hypothetical, both models represent a mechanism that is also found in extant analogues, fit with the available information on the anatomical features of the pterosaurian forelimb, and lay down a basis for further biomechanical and aerodynamical investigations.

III. Growth strategy and life history of *Rhamphorhynchus* inferred from bone histology of an ontogenetic series

The most commonly found pterosaur remains in the Solnhofen limestones belong to the well-known genus *Rhamphorhynchus*, among which there is a striking variability in body size. Originally Wellnhofer (1978) described five different *Rhamphorhynchus* species, which later on proved to be a single species represented by specimens of different ontogenetic stages (Bennett, 1995). Based on the apparent diversity of ontogenetic stages in the fossil record it has been suggested that, unlike most extant birds and mammals or derived pterodactyls (Ricqlès et al. 2000; Steel, 2008), *Rhamphorhynchus* must have had slow, crocodile-like indeterminate growth with at least three years of growth after they had first become airborne (Bennett, 1995; Chinsamy et al. 2008). Furthermore it has been proposed that, based on morphological characters, all known specimens including the smallest ones could fly, i.e. they were precocial fliers (Bennett, 1995, Unwin 2005; Lü et al. 2011). This precocial-hypothesis has been brought to its extreme by Unwin (2005) and Lü et al. (2011) who extended the hypothesis of early flight abilities to pterosaurs in general and suggested that they were superprecocial which refers to their ability to fly and take care of themselves immediately after hatching.

In contrast, already the first histological studies of earlier pterosaur genera as well as that of *Rhamphorhynchus* (Padian et al. 2004) and more derived pterodactyls indicated growth rates that were comparable to those of birds or mammals rather than those of extant crocodiles, so growth could not have protracted over several years (Ricqlès et al. 2000; Padian et al. 2004). Hence, the results of histological studies all implied that high growth rates and basal metabolic rate characterized pterosaurs in general (Ricqlès et al. 2000; Padian et al. 2004; Steel, 2008).

So far growth strategy of *Rhamphorhynchus* has been assessed based mainly on macromorphological characters, whereas only one study concentrated on the microstructural features of the bones to reveal life history traits of this genus (Padian et al. 2004). Here I present the first histological survey of an ontogenetic series of *Rhamphorhynchus*.

Materials and methods

Five specimens of *Rhamphorhynchus* that can be ordered in an ontogenetic series were sampled for this study. Bone samples were thin-sectioned into transverse sections using standard techniques. Histological features of the selected bones were studied under polarized light microscope. Wingspan and body mass estimates were used as measures of size to correlate histological features of each specimen to its relative body size. Wingspan estimates were performed in CorelDRAW 12 using own reconstructions, whereas body masses were calculated based on the equation given by Witton (2008). On the basis of the observed histological features of *Rhamphorhynchus* I tested whether Bennett's (1995) three size-classes indeed reflect real ontogenetic ages. Taking all results into account I assessed the most plausible growth rate and life history strategy of *Rhamphorhynchus*.

Results and conclusions

- Bennett's (1995) second size category contains subadults as well as adults, thus it does not reflect real ontogenetic stage.
- Developmental plasticity seems to occur regarding body size of histologically as well as macromorphologically adult specimens.
- Contrasting the expected effects of the 'superprecocial flier' hypothesis, hatchlings sustained high initial growth rate, however only up to the attainment of a considerable low proportion of adult body size.
- The early fast growth phase was followed by a prolonged, reptilian-like slow-growth phase; the onset of powered flight is considered here as the cause of this transition.
- The similar histological pattern of *Pterodaustro* is also the result of the onset of flight and not of reproduction.
- Rapid growing early juveniles were either attended by their parents or they were immediately independent, precocial but not volant, hiding creatures until attaining a certain somatic maturity to get airborne.

- Although EFS is absent in all investigated specimens, due to the restricted sample size neither determinate nor indeterminate growth strategy could be confirmed in *Rhamphorhynchus*.
- Histological studies shed light on the diversity rather than a universal pattern of pterosaurian growth strategies.

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